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RESPIRATORY ADAPTATIONS TO THE OXYGEN MINIMUM LAYER IN THE BATHYPELAGIC MYSID *GNATHOPHAUSIA INGENS*

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Zones of minimum oxygen are found at intermediate depths in most of the world's oceans and, although the dissolved oxygen in some of these "oxygen minimum layers" is considerably less than 0.5 ml/l, populations of metazoans exist there (Schmidt, 1925; Sewell and Fage, 1948; and Banse, 1964). Previous studies have shown that two crustaceans which live in such minimum layers are unusually effective at removing oxygen from water (Teal and Carey, 1967; Childress, 1968a). One of these organisms, the lophogastrid mysid *Gnathophausia ingens,* is apparently capable of living largely aerobically at oxygen concentrations as low as 0.20 ml O_2/l (Childress, 1968a). The ability to regulate oxygen consumption down to this low level is shared with other inhabitants of the oxygen minimum layer (Childress, 1968b and 1969) and is unique among previously studied metazoans.

The relationship between crustacean respiratory adaptations and physiological mechanisms such as ventilation rates and utilization of available oxygen have been investigated only in a few species of crustaceans inhabiting regions with abundant oxygen (Thomas, 1954; Larimer and Gold, 1961; Arudpragassam and Naylor, 1964; Moshiri, Goldman, Godshalk and Mull, 1970). This report examines the adaptive mechanisms that allow *G. ingens* to be so effective in the regulation of its oxygen consumption rate at low oxygen concentrations.

Methods and Materials

Animals

Most of the specimens of *Gnathophausia ingens* (Dohrn, 1870) used were taken in the basins off southern California with a ten foot Isaacs-Kid midwater trawl from the Research Vessel Velero IV. However, some of the specimens used were captured in the same region with a six-foot-square Tucker trawl from the Research Vessel Te Vega. Immediately after they reached the surface, the animals were placed in one gallon polyethylene jars which were full of cold (3° C) seawater. The animals were then transported to either Hopkins Marine Station or the Santa Barbara Marine Laboratory where they were maintained in seawater at 5 to 7.5° C. Individuals of *G. ingens* have now been maintained for more than a year on a diet of salmon, shrimp and bonito. All of the experimental animals were sexually immature individuals of undetermined sex and had a wet weight less than 13 g.

Respiration measurements

Oxygen consumption rates at different oxygen concentrations were determined for individuals sealed in a chamber filled with seawater and maintained at 5.5 ± 0.1° C by means of a refrigerated water bath. The inner part of the chamber to which the animal was exposed was constructed of pyrex with a lucite lid. The rate of change in oxygen partial pressure in the chamber was continuously measured with a Clark-type oxygen electrode (Clark, 1956) as the animal reduced the oxygen partial pressure from air saturation to unmeasurably low partial pressures (less than about 0.1 mm Hg). The time required for this reduction ranged from 12 to 32 hours. The electrode tip was enclosed in a perforated plastic vial containing a magnetic stirring bar which stirred the electrode and the contents of the chamber. To avoid excitation of experimental animals by light, the experimental chamber was kept in darkness during each experiment. To control pH, I used seawater buffered with 2.5 g per liter of tris(hydroxymethyl)amino-methane adjusted to pH 8.0 with HCl, and diluted to the appropriate osmolality with distilled water. To test the effect of waste product accumulation on the respiration of experimental animals, the chamber was filled with water saturated with 95 per cent oxygen and 5 per cent carbon dioxide. Since there was more oxygen in the chamber, the animals could be maintained in the chamber about five times longer than usual. This should have resulted in a build-up of far more waste products during the course of the experiment. Yet the data obtained were indistinguishable from those obtained by the usual method. Therefore it was concluded that waste product build-up did not affect the results.

Streptomycin (6 mg/l) and aureomycin (20 mg/l) were added to the seawater to minimize microbial growth. As a control on microbial respiration, the animal was removed from the chamber at the end of each experiment, air-saturated seawater was added to replace the volume of the animal, and the rate of oxygen consumption in the chamber was again measured for 3 to 24 hours. These rates, which were independent of oxygen concentration, constant with respect to time and always less than 5 per cent of the total measured rate, were subtracted from the respiratory rates measured with the animal in the chamber, to obtain the respiratory rates of each animal. The rate of maximum activity was measured by using a chamber without the plastic sieve that shielded the animal from the stirring bar. The bar was then operated at the highest speed that still allowed the animal to maintain its position in the chamber.

The oxygen electrodes were polarized at 0.7 v by means of a voltage divider and an "alkaline" type battery, and the resulting potential difference across a 20 kohm potentiometer was continuously recorded on potentiometric stripchart recorders. The electrodes were calibrated before and after each run with air-saturated and nitrogen-saturated seawater (99.99%) at the experimental temperature. If the initial and terminal air calibrations differed by more than 2%, or if the nitrogen calibrations differed measurably, runs were discarded. Rates of oxygen consumption were calculated using the oxygen solubility tables of Green and Carritt (1967). Because the animals were excited by handling, the recordings during the first 5 to 6 hours were disregarded.

Since oxygen electrodes are very sensitive to stirring, it was possible to measure the swimming activity of an animal by fastening the animal in one posi-

tion and placing an oxygen electrode near the animal's pleopods. The activity and respiratory rates of animals were monitored simultaneously in several runs by fastening the animal in the above manner in a respiration chamber containing a second, isolated electrode agitated by a stirring bar. The animal's activity was indicated by the difference in readings between the animal-stirred electrode and the electrode stirred at a constant rate by the magnetic stirrer.

Respiratory rate, oxygen in exhaled water, and flow rate of water over the gills were measured simultaneously in the following manner. The animal's head was placed in a cylindrical plastic vial and a piece of rubber balloon sealed the animal to the vial. Water was drawn in under the carapace, passed through the gills and then pumped out of the carapace into the vial where it first passed a Beckman Macro Oxygen Electrode and then a thermistor flowmeter. The term ventilation volume will be used to refer to the rate of volumetric flow of seawater over the gills. The flowmeter was a thermistor probe (Yellow Springs Instrument Co. model 403) with 30 inches of 30-gauge nichrome wire wrapped around the tip and insulated with epoxy enamel. This wire was heated with 400 ma at 3 volts and the resulting thermistor temperature was proportional to the flow rate past it. The flowmeter was calibrated by measuring the amount of water that had run past it in a given period of time. The precision of the flowmeter was about ±10% between 0.5

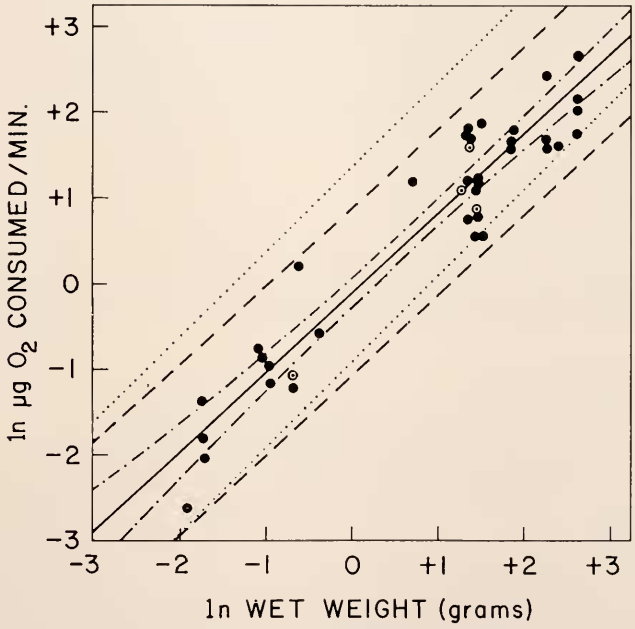

FIGURE 1. Relation between (ln) size and (ln) respiration (lowest sustained rates, see text) in *Gnathophausia ingens* at 5.5° C; ———— regression line ln $R = -0.105 + 0.925$ ln W, $R = 0.900\ W^{0.925 \pm 0.10}$, – · – · – · – · – 95% confidence interval for mean R at given W, – – – – – – – – – – 95% confidence interval for individual R at given W, ... envelope around all measured respiration rates; for upper line respiration equals 3.6 mg/kg/min, for lower line respiration equals 0.4 mg/kg/min, ⊙ means that two data points are at that locus, • means that a single datum point is at that locus.

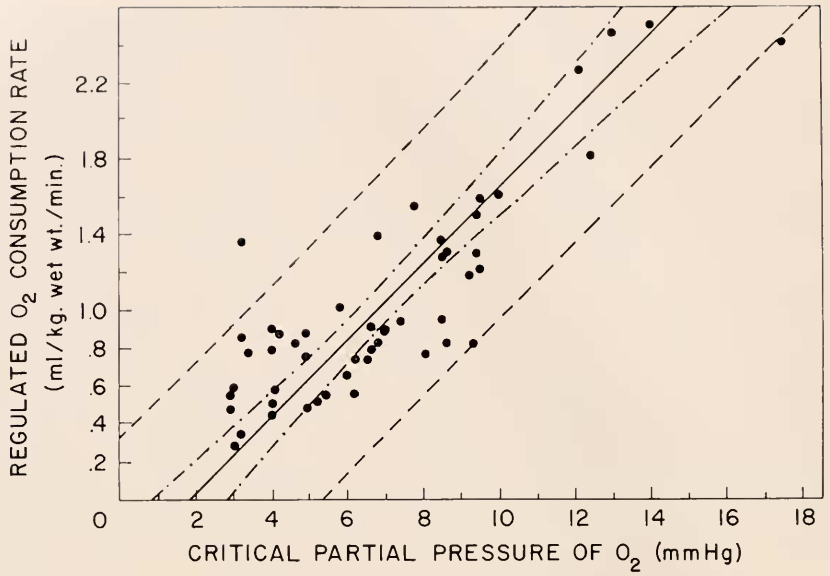

FIGURE 2. Relationship between respiration and P_c in *Gnathophausia ingens*; ———— regression line $X = 4.973\,Y + 1.798$ (X as dependent variable) 95% confidence 4.973 ± 0.889, 1.798 ± 0.470; $r = 0.85$, - · - · - · - · - 95% confidence interval for mean X at a given Y, – – – – – – – – – 95% confidence interval for individual X at a given Y. Regulated oxygen consumption rate is defined as the lowest rate sustained for more than 10 minutes between 20 and 70 mm Hg of oxygen. Critical partial pressure (P_c) is defined as the partial pressure of oxygen at the point where the lowest sustained rate intersects the dependent part of the curve or its extension.

and 50 ml/minute. Flow rate was also calculated from the measured oxygen consumption rate and the amount of oxygen removed as the water passed over the animal's gills. A Beckman Macro Electrode was used to monitor oxygen in exhaled water because this electrode is insensitive to variations in flow rate.

RESULTS

Oxygen consumption rate

The respiratory rates measured during a single run varied a great deal, probably due to "spontaneous" variations in the experimental animal's activity. This variation made it extremely difficult to assign a single representative value for the respiratory rate of an animal for the duration of a given experiment. *Gnathophausia ingens* is a very active and readily excited animal, and the lowest activity which it usually shows in the laboratory is slow swimming. For this reason, I have used the lowest sustained (*i.e.*, sustained for at least 10 minutes) rate between the oxygen partial pressures of 20 and 70 mm Hg as the "assigned" respiratory rate for a given run. These rates were plotted against the wet weight of the animal and the regression equation of oxygen consumption as a function of wet weight was fitted by the least squares method (Fig. 1). The equation determined for 42 experiments with 26 animals was $R = 0.90\ W^{0.93 \pm 0.10}$ where $R = \mu g\ O_2/min$ and $W =$ wet weight in grams.

The exponent of the weight was not significantly different from 1.0, the exponent for weight specific respiration ($P < 0.05$). Consequently, all subsequent data are presented on a wet weight specific basis.

In those runs where respiration and activity were measured simultaneously the respiratory rate of nonswimming animals was between 0.40 and 0.45 mg O_2/kg wet wt/minute. The "active" rate, determined for 5 animals, was between

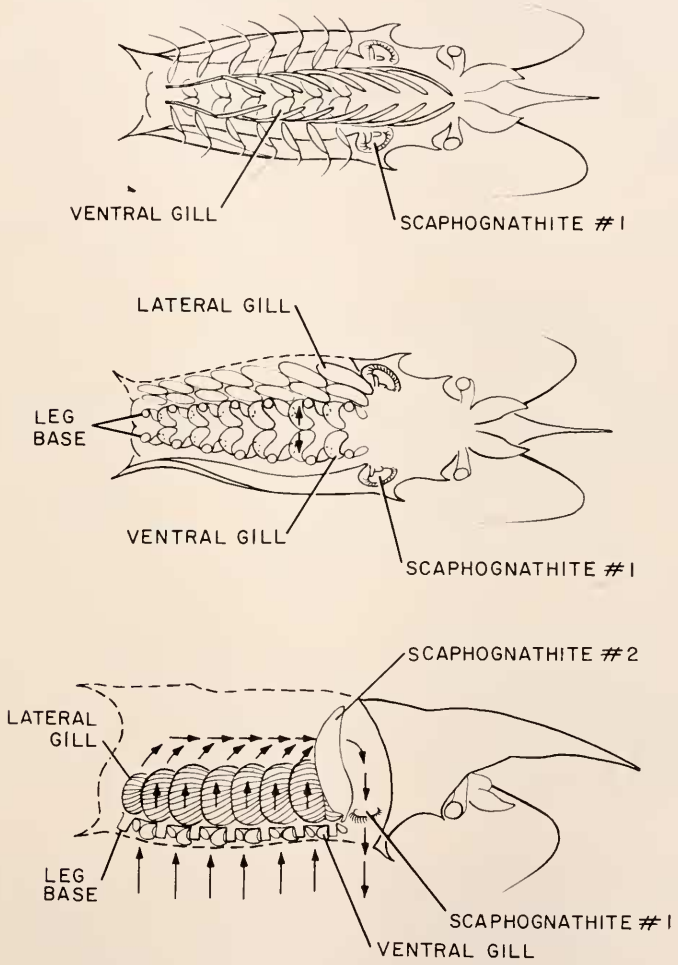

FIGURE 3. (A.) Ventral view of the cephalothorax of *Gnathophausia ingens*. Water is drawn between the legs midventrally into the ventral gills. Scaphognathite 1 is the expodite of the second maxilla. Scaphognathite 2 is the epipodite of the first trunk limb. (B.) Ventral view of the cephalothorax of *G. ingens* with legs and one side of the carapace removed (schematic representation not absolutely accurate). The respiratory water passes laterad through the ventral gills, then turns dorsad and flows through the lateral gills. (C.) Side view of the cephalothorax with the carapace removed (position indicated by dashed line). The respiratory water (indicated by arrows) passes in a dorsal direction through the lateral gills. It is then pumped forward, down and out of the carapace by the two scaphognathites.

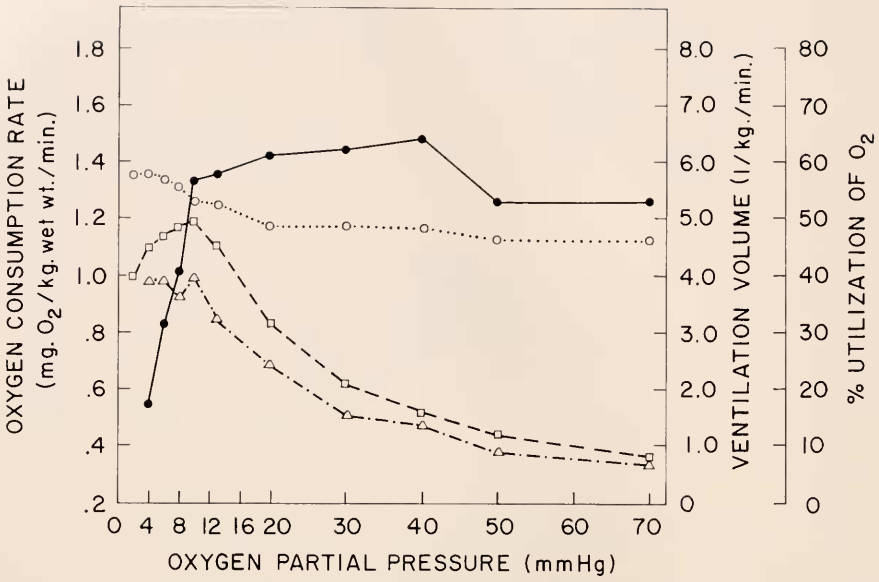

FIGURE 4. Oxygen consumption rate, per cent utilization of oxygen, and ventilation volume in *Gnathophausia ingens* as functions of oxygen partial pressure, mean of 8 runs; ———— oxygen consumption rate, ... % utilization =

$$\frac{PO_2 \text{ of inhaled water} - PO_2 \text{ of exhaled water}}{PO_2 \text{ of inhaled water}} \times 100\%$$

– – – – – – – – measured ventilation volume, – · – · – · – calculated ventilation volume =

$$\frac{O_2 \text{ consumed/min}}{O_2 \text{ removed/l water passed over gills}}$$

2.6 and 3.6 mg O_2/kg wet wt/minute. Visual observations of individuals in the respiration chamber suggested that a respiratory rate of about 0.8–0.9 mg O_2/kg wt wt/minute (approximately the same as the rate expressed in the regression equation) corresponded to a slow rate of swimming just sufficient to allow the animal to maintain its position in the water column.

Regulation of oxygen uptake

The ability of *G. ingens* to regulate its oxygen uptake was studied in 50 runs with 34 animals of between 0.14 and 13 g wet weight. Although *G. ingens* has been shown to regulate its respiratory rate to a very high degree (Childress, 1968a), a single critical partial pressure (P_c) below which the species does not regulate cannot be defined because the P_c varies with the respiratory rate and the respiratory rate is quite variable (due to activity variations). This relationship is shown in Figure 2. Experimental animals continued to consume oxygen at partial pressures below the P_c until no oxygen was detectable in the chamber; but they continued swimming for less than 30 minutes after they had exhausted the supply of oxygen. These animals could be revived with aerated water up to 6 hours after their supply of oxygen had been exhausted.

Path of respiratory water flow

The resipratory currents of *G. ingens* were traced by placing water containing dyes at different points around the carapace of living animals and observing the path taken by the dye. Most of the respiratory water entered between the left and right sets of legs into the ventral gills (Fig. 3); it passed laterally through the ventral gills and into the lateral gills. The water then passed dorsally through the lateral gills, flowed anteriorly above them, and then turned downward and passed out through the exhalant openings. No water entered under the posterior dorsal edge of the carapace. A little may enter at the base of the thoracic exopodites. The structures responsible for this water flow are the two pairs of scaphognathites. The anterior scaphognathite on each side is the exopodite of the second maxilla; the posterior one is an epipodite on the first thoracic limb.

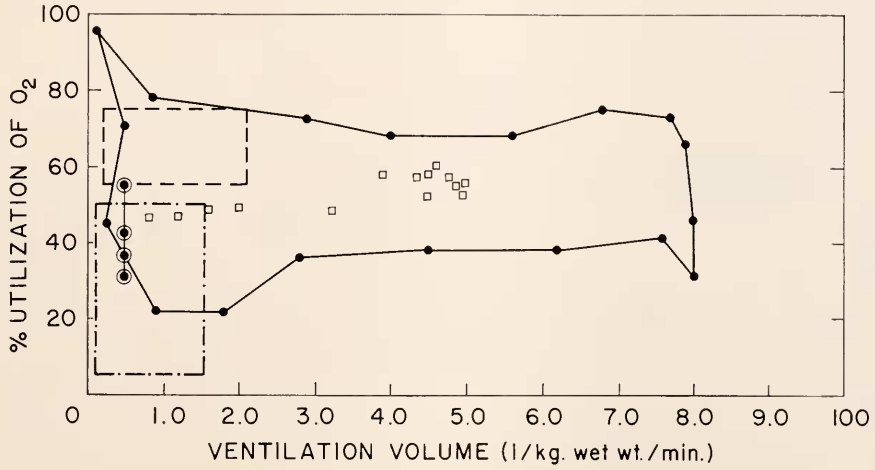

FIGURE 5. Relation between percent utilization and ventilation volume in *Gnathophausia ingens*; □ *G. ingens*—mean points taken from Figure 21, •————• *G. ingens*—envelope enclosing all values found, – – – – – – – – – – *Procambarus simulans*, from Larimer and Gold (1961) – · – · – · *Carcinus maenas*, from Arudpragassom and Naylor (1964), ⊙————⊙ *Homarus vulgaris*, from Thomas (1954).

The illustrations of the gills diagrammatically simplify their very complexly branched and foliaceous structure (Fig. 3). The gill surface area is certainly extremely large; but, because of the great irregularity of the smaller gill divisions, it was not possible to make a satisfactory quantitative estimate of the gill surface area.

Mechanics of oxygen uptake

Ventilation volume, per cent utilization, and oxygen consumption were measured in a series of 8 runs using 6 different individuals between 6 and 8 g wet wt (Fig. 4). Individual *G. ingens* had a low ventilation volume at higher oxygen partial pressures and increased this ventilation volume at lower oxygen

levels. The disagreement between the calculated and measured flow rates is probably a result of the combined errors of the two oxygen electrodes and the flowmeter. The highest ventilation volume generally occurred at the P_c, but ventilation remained high until all of the oxygen was consumed. Although the mean curve showed a rather constant per cent utilization, at lower oxygen partial pressures, it actually increased slightly in some cases and decreased slightly in others.

The presentation of these data in Figure 4 masks the short-term changes in the different parameters. Figures 6 and 7 show two sections of recordings on which Figure 4 is based. These recordings show that individuals of *G. ingens* ventilated intermittently at oxygen partial pressures above 15–20 mm Hg and

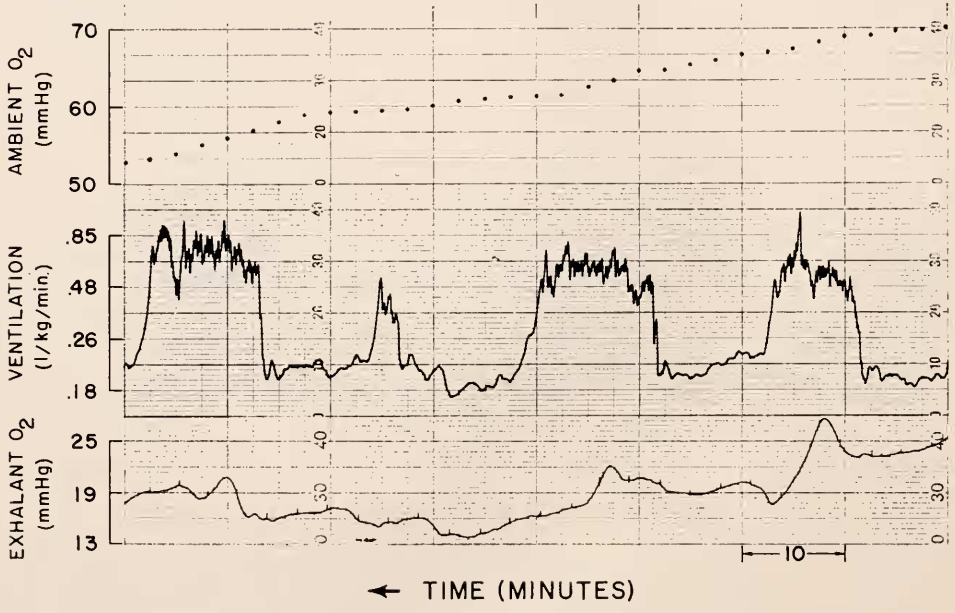

FIGURE 6. Recordings of ventilation volume and exhalant oxygen and an abstraction of the recording of oyxgen in the chamber (Ambient O_2).

pumped continuously below this level. These recordings also show that, in the short-term, higher ventilation volumes were usually associated with lower per cent utilization.

DISCUSSION

Most crustaceans previously studied have a respiratory rate which, unlike that of *G. ingens,* is proportional to body surface area (Wolvekamp and Waterman, 1960). However, *Euphausia pacifica,* the other extensively studied pelagic crustacean, has a respiratory rate that is directly proportional to weight (Paranjape, 1967; Small and Hebard, 1967). The respiratory rate of *G. ingens* is clearly not surface proportional, but the 95% confidence interval is broad enough that it is not significantly different from either the intermediate proportionality

found for a series of arctic and tropical crustaceans by Scholander, Flagg, Walters and Irving (1953) or from weight proportionality. The significance of weight-proportional (or nearly weight-proportional) respiration in pelagic crustaceans is not clear.

The absolute value of *G. ingens*' respiratory rate is rather low compared to crustaceans previously examined (Wolvekamp and Waterman, 1960; Childress, 1968b). This may well be an adaptation to the paucity of food in the deep-sea (Childress, 1971). The nine-fold range of metabolic rate in *G. ingens* is comparable to that of free-swimming fishes (Brett and Sutherland, 1965) and somewhat higher than is usual for crustaceans. Presumably this wide respiratory

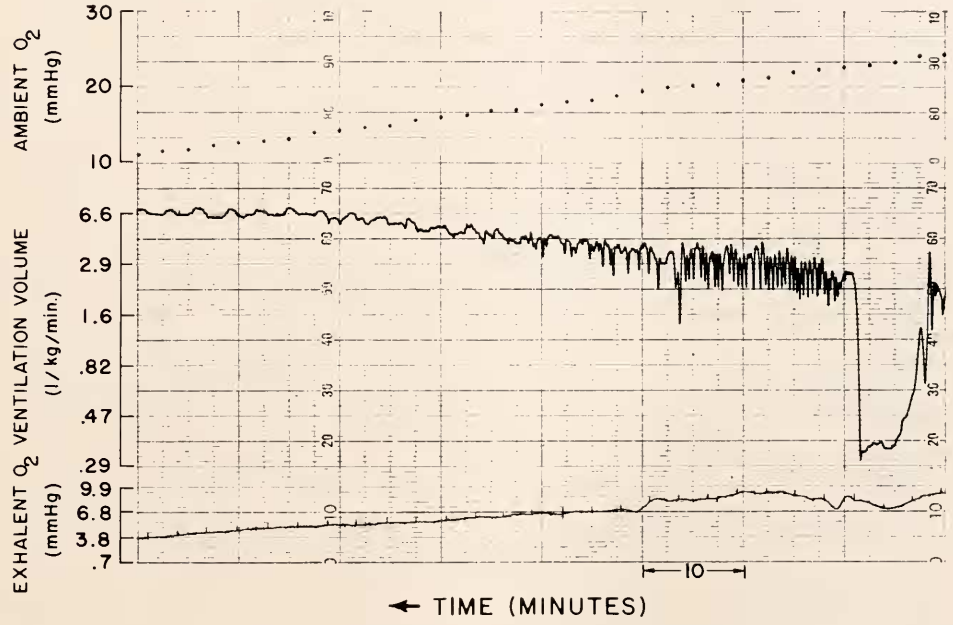

FIGURE 7. Recordings of ventilation volume and exhalant oxygen and an abstraction of the recording of oxygen in the chamber (Ambient O_2). (The pattern seen in the ventilation volume recording at oxygen partial pressures below about 11 mm Hg is not due to the animal but is a result of fluctuations in the heater voltage source.)

range allows the animal to conserve energy by slow swimming most of the time while retaining the capacity for extremely rapid swimming either to capture prey or to escape predators.

The direct proportionality between the P_c and respiratory rate might be expected but it has not previously been demonstrated for invertebrates or fishes. This proportionality offers the possibility of gaining insight into the *in situ* respiratory rate of *G. ingens*. Since this species lives continuously and grows in the oxygen minimum layer off the southern California coast and yet has very little anaerobic capability, it must live largely aerobically at oxygen partial pressures around 6 mm Hg (Childress 1968a, 1968b, 1969 and in preparation). The present data show that at this oxygen level the mean respiratory rate cannot exceed

about 0.8 ± 0.1 mg O_2/kg wet weight/min. Visual observations suggest that this respiratory rate corresponds to slow swimming by the animal (approximately the minimum level of swimming activity required for individuals to maintain their position in the water column). It seems likely therefore that individuals of this species when in the minimum layer spend most of their time respiring at about 0.8 mg/kg/min, swimming just rapidly enough to maintain their position in the water column, and relying on anaerobic metabolism for short bursts of greater activity.

Manton (1928) has hypothesized on the basis of preserved specimens of *G. ingens* that the respiratory current flow in this species resembled that in the neritic mysid *Hemimysis lamornae*. She proposed that the main flow of respiratory water enters *G. ingens* (as it does in *Hemimysis* and all other previously studied mysids) under the posterior dorsal edge of the carapace. My observations disagree with Manton's hypothesis showing instead that almost all respiratory water enters the gills in the ventral mid-line and proceeds laterally and dorsally through the gills (Fig. 5). This observed pattern of flow passes all of the respiratory water through the gills and provides a relatively long path-length through the gills. Although I was unable to measure the surface area of the gills because they are very complex and irregular, it is obvious that *G. ingens* has a very large gill surface area compared to crustaceans that live in higher oxygen partial pressures (including *Gnathophausia gracilis*, *Gnathophausia gigas* and adult females of *G. ingens*). However, the gills of *G. ingens* appear roughly comparable in size to those of caridean and peneid decapods which inhabit the minimum layer. Unusually large gills have also been found in fishes that occur in the oxygen minimum layer (Parin, 1961, Ebeling and Weed, 1963; Gibbs and Hurwitz, 1967). This large surface area is undoubtedly an important factor in explaining the ability of *G. ingens* to extract oxygen so effectively.

The pattern or respiration, ventilation and per cent utilization of oxygen shown in Figure 4 contrasts sharply with that found in studies of crustaceans that inhabit waters high in oxygen (Thomas, 1954; Larimer and Gold, 1961; Arudpragassam and Naylor, 1964, Moshiri *et al.*, 1970). In particular these species use their maximum ventilation volume at or near air saturation and as the oxygen partial pressure is reduced the ventilation volume either decreases or remains constant. The per cent utilization in these species is roughly independent of ventilation volume and either remains constant or increases as the oxygen partial pressure decreases. *G. ingens*, however, holds its per cent utilization relatively constant as the oxygen partial pressure is reduced and regulates its removal of oxygen from the water by greatly increasing its ventilation volume at lower oxygen partial pressures. In addition *G. ingens* can pump far more water over its gills than can any crustaceans previously examined and extract as much or more oxygen from the water in the process (Fig. 5).

The maximum ventilation volumes observed in fishes (Saunders, 1962) correspond roughly to the maximum volumes shown by individuals of *G. ingens*. However, *G. ingens* is vastly superior in regulatory ability to these fishes because ventilation volume and per cent utilization are inversely related in fishes (Fry, 1957; Saunders, 1962; Holeton and Randall, 1967) but independent of one another in *G. ingens* and other crustaceans. Therefore, although at the maximum ventilation volume a fish may be able to pump as much water over its gills

as can an individual of *G. ingens*, the individual of *G. ingens* can remove two to six times more oxygen from the water. The inverse relation between ventilation volume and per cent utilization in fishes has been attributed to deformation of gill lamellae away from optimal positions at higher flow rates. It may well be that the characteristic independence of these parameters in crustaceans is due to the greater rigidity (readily observed in gross dissection) of crustacean gills, which are covered with exoskeleton.

Another important difference between the regulatory patterns of fishes and of *G. ingens* is that the P_c of fishes usually corresponds to a precipitous drop in ventilation volume (Beamish, 1964; Holeton and Randall, 1967), while the P_c in *G. ingens* corresponds to a plateau or slight decline in the ventilation volume. This pattern suggests that the failure of respiratory regulation in fishes is the result of the failure of some internal mechanism to function at low internal oxygen levels. The failure of *G. ingens* to regulate below its P_c, however, may simply result from reaching the animal's maximum sustainable ventilation volume. This combined with the relatively constant per cent utilization causes a decrease in respiratory rate proportional to the decrease in oxygen concentration (dependent respiration) below the P_c.

The remarkable adaptation of *G. ingens* to living at low oxygen partial pressures is strikingly indicated by the fact that individuals need not ventilate continuously until the environmental oxygen partial pressure falls to less than 20 mm Hg.

That extreme aerobic adaptations do not characterize animals of the intertidal mud-flats, which often encounter anoxic conditions, or other neritic or fresh water species seems surprising at first. However, these extreme adaptations are probably peculiar to residents of the oxygen minimum layer because its stability has allowed its residents to evolve aerobic adaptations to survive in a very low oxygen environment and thereby take advantage of the energy bonus of aerobic as opposed to anaerobic respiration. On the other hand, oxygen partial pressures in other low oxygen habitats fluctuate widely, often rapidly giving way to total anoxia. Therefore residents of these other low-oxygen habitats either breath air or endure temporary anaerobiosis but do not effectively extract oxygen at low partial pressures. Because oxygen partial pressure in the oxygen minimum remains constantly low, its residents can not repay a considerable oxygen debt, and therefore they lack adaptations allowing for extended periods of anaerobiosis. A possible exception might be a resident, such as a parasite, with a superabundant food supply. Non-resident, "visiting" species in the oxygen minimum which include diel vertical migrators or resting stages (Longhurst, 1967) may be adapted anaerobically. Such adaptations would impose on them no requirement for extra energy because anaerobic end-products could be metabolized during the period of time that they spend out of the oxygen minimum layer.

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Summary

1. The oxygen consumption rate in *G. ingens* is not surface proportional, but is not significantly different from weight proportionality or intermediate proportionality.

2. The critical partial pressure of oxygen in *G. ingens* is directly proportional to the regulated oxygen consumption rate. This relationship suggests that a respiratory rate of about 0.8 ml O_2/kg wet wt/min (corresponding to a slow rate of swimming probably just sufficient to allow an individual to maintain its depth in the water column) is the maximum which *G. ingens* can sustain over long periods *in situ* in the minimum layer.

3. Respiratory water enters the gills along the ventral midline, travels through them first laterally and then dorsally, finally exiting past the two scaphognathites located anterior to the gills. No respiratory water enters at the posterior dorsal margin of the carapace. The large gill surface of *G. ingens* is almost certainly an important factor in its unusual aerobic abilities.

4. The ability of *G. ingens* to maintain a high ventilation volume and a high per cent utilization independent of each other is certainly important in explaining its aerobic abilities. The regulatory abilities of *G. ingens* are probably limited by its maximum ventilatory abilities.

5. It is suggested that the extreme stability of the deep sea made possible the evolution of the specialized aerobic adaptations found in *G. ingens*. This situation contrasts sharply with that of inhabitants of less stable low oxygen environments as well as "commuters" in stable low oxygen environments which can temporarily use anaerobic metabolism without an energy penalty and which would therefore gain negligible selective advantage from specialized aerobic adaptations.

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